

**A MOST STRIKINGLY MYRMECOMORPHIC MIRID FROM  
AFRICA, WITH SOME NOTES ON ANT-MIMICRY AND  
CHROMOSOMES IN HALLODAPINES  
(MIRIDAE, HETEROPTERA)**

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*Abstract.*—The remarkably myrmecomorphic characters of the hallodapine mirid *Leaina belua* Linnavuori from West Africa are described and illustrated and some comparisons made with other antlike mirids exhibiting supposed imitations of orthopteroid mandibles. Some literature on the possible role of ant mimicry in Miridae and Alydidae is reviewed. A plea is made for detailed observations on the biology of those hallodapines that display the highest degree of myrmecomorphy. Attention is further paid to the exceptionally low number of chromosomes ( $n = 2$  and  $4$ ) in some hallodapines investigated by the author.

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In February 1982 I sent copies of Figures 1-3 (except Fig. 2f) presented in this paper to 17 heteropterists, including several mirid specialists, in order to better inform myself about the taxonomic status of this remarkable mirid from West Africa. As the male genitalia (Fig. 3) indicate, it clearly belongs in the Phylinae, Hallodapini. Because I am not a mirid specialist, I wanted to be sure whether the species was already described before preparing a short note on its exceptional cephalic modifications, which give the illusion of the head of an ant. Of the several replies to my question, two colleagues (Dr. Akingbohunge, Nigeria, and Dr. Linnavuori, Finland) informed me that the animal in question already had a name. It was described by Linnavuori (1974) as *Leaina belua* new genus and species (Hallodapinae<sup>1</sup>) based on material from the Ivory Coast. Although Linnavuori mentioned the remarkably antlike habitus in his formal description of the genus and species, the phenomenon remained somewhat hidden in his taxonomic treatment of many other new taxa. Therefore, it may be of general interest to focus special attention on it in this commemorative issue at the occasion of Dr. Froeschner's seventieth birthday. I will not detail the vast literature on "ant mimics" in Heteroptera. My only hope is that this note will stimulate biologists to make careful observations on the biology of this and other ant like forms in Africa and elsewhere and to set up experiments for analyzing the functional significance, if any, of myrmecomorphy.

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<sup>1</sup> Linnavuori followed Wagner (1970) in giving the hallodapines subfamily rank. I agree with Schuh (1974:292) that this position "has little merit, because it is based only on the superficial uniqueness of the group." It would moreover cause the family to be split up in an endless mass of subfamilies if this procedure were followed consistently.

STRUCTURAL PECULIARITIES OF *Leaina belua*  
AND SOME OTHER PHYLINAE

The single male that came to my disposal originated from the Ivory Coast, Katiola savanne, 54 km N of Bouaké, 26.XI.1980. It was caught in a pit-fall trap (KAS 2) during a large-scale sampling survey for studying residual effects of insecticides on invertebrates after tsetse fly control by aerial spraying. This program was supervised by the Department of Toxicology (Wageningen). Mr. J. Everts, coordinator of the program, made part of the samples which were separated in Africa by insect order, available to us. It is not surprising that the mirid bug was stored in a vial with otherwise only small Hymenoptera. Dr. Akingbohunge informed me that he has in his collection the same species, collected in Nigeria, Ilora, in the derived savanna area of Oyo state (2 males in Malaise trap, 19.VIII.1974, J. T. Medler collector).

After the single male was compared with the description of *L. belua*, the length of the labium appeared to be different. According to Linnavuori (1974), the rostrum should extend to the metasternum, whereas in our specimen it does not surpass the first coxae (Fig. 1). This latter condition, however, holds also for the holotype male of *L. belua*, which I was able to study. Small differences between Linnavuori's and my figures of genitalia may be due to different angles of viewing, so I consider the male at hand conspecific with *L. belua*.

The most striking myrmecomorphic traits of this species are found on the head. The general facies of the insect in dorsal view (Fig. 2a) is shared by many other antlike Miridae: eyes removed from pronotal margin, convex connection of head with anteriorly narrowed pronotum, wing margin sinuate, white fascia medially on the brownish corium, and abdomen globular and constricted at base. Sex-related brachyptery is another phenomenon often associated with myrmecomorphy; the wings of the female of *L. belua* are said to be strongly reduced. The dramatic deviations from the generalized mirid head (Fig. 1a) become apparent in frontal (Fig. 2d) and lateral views (Figs. 1, 2b, c). The head is diagnosed as follows: proportionally large, elongate with narrow neck; narrow ellipsoid eyes; antennal sockets situated between anterior edges of eyes; ventral surface of head strongly excavated laterally, the buccular region forming a thin keel-like vertical plate, this large foliaceous buccular expansion tightly encompassing the first labial segment. The unique cephalic structure involves the enlargement and elongation of the genae anteriorly, extending sharply triangularly beyond apex of the partly concealed clypeus. The external margin of the gena is formed by a sharp horizontal carina starting from the upper anterior edge of the eye. These dark-colored genal transformations are reminiscent of orthopterous mandibles, at least to an entomologist, particularly in lateral view. As a consequence of these outgrowths and the keel-like projection of the gular region, the limits between lora and buccula are indistinct; remnants of them are visible underneath the genae (arrow in Fig. 2c). The antlike shape of the head is further enhanced by the long, laterally flattened, scapus-like second antennal segment, which is bent elbow-like with respect to the remaining slender segments (Fig. 1). It is not known whether the antennae are kept folded in living specimens. Note further that the labrum and labium are short and inconspicuous.

In any larger treatment of the diverse family Miridae the term myrmecomorphic

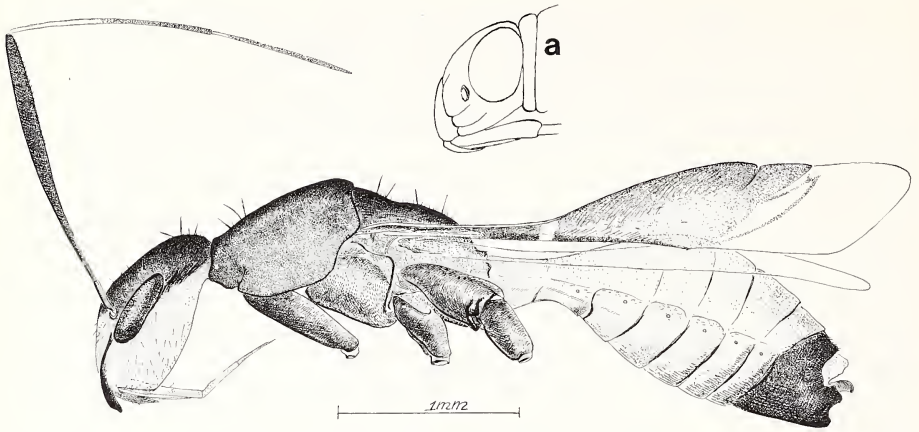


Fig. 1. *Leaina belua*. Left lateral view of male, legs omitted. a, lateral view of generalized mirid head.

is encountered repeatedly (e.g., Slater and Baranowski, 1978; Schuh, 1974; Wagner and Weber, 1964; Kullenberg, 1946). Particularly, the Phylinae of the Old World tropics as illustrated in the revisions of Schuh (1974, 1984) and Orthotylinae and Mirinae in the Neotropics show a multitude of morphological adaptations producing antlike appearance not equalled in any other family. From such analyses it also becomes clear that antlike mirids have evolved independently many times. What struck me most in reading the work of Schuh was that a kind of cephalic type described here for a hallodapine seems to reach a pinnacle in two other tribes of the Phylinae. Schuh (1974:258-259) stated: "In certain undescribed genera in the Pilophorini and Leucophoropterini the gula [*sic*] is carinate below the eye and gives the appearance of mandibles when viewed anteriorly. All of these structural characteristics have evolved more than once and are therefore indicative of the extreme adaptability of the Miridae to ant-mimic selection." However, on page 305 in the same work and dealing with the Leucophoropterini, Schuh speaks of the carinate gena forming a broad ridge below the eye, indicating a lapsus in the statement above.

Another example in the Phylinae where structures have evolved that remind us of orthopteroid mandibles should be noted. Mr. Dolling wrote me after he had compared my illustrations of the then unknown hallodapine with material in the BM collections: "In many Hallodapini the labrum is very broad in the vertical plane." I sorted, in the Tervuren collections, a series of unidentified species from Africa that reveals this vertical dilation of the labrum in various degrees. In the most extreme case I have seen, the labrum appears like a thin blade through lateral compression (Fig. 2f, f'). Although unpaired, this development could have the advantage over the paired outgrowths in *L. belua* that it is movable and supposedly more efficient if it indeed functions for advertisement. In contrast to *L. belua*, all these bugs with an enlarged labrum have a solid, long rostrum. An enlarged laterally flattened labrum occurs also in the New Guineaian genus *Gulacapsus* Schuh, Phylinae, Leucophoropterini (see Schuh, 1984:230), and in the African hallodapine genus *Skukuza* Schuh, 1984 (Fig. 62 in Odhiambo, 1959).

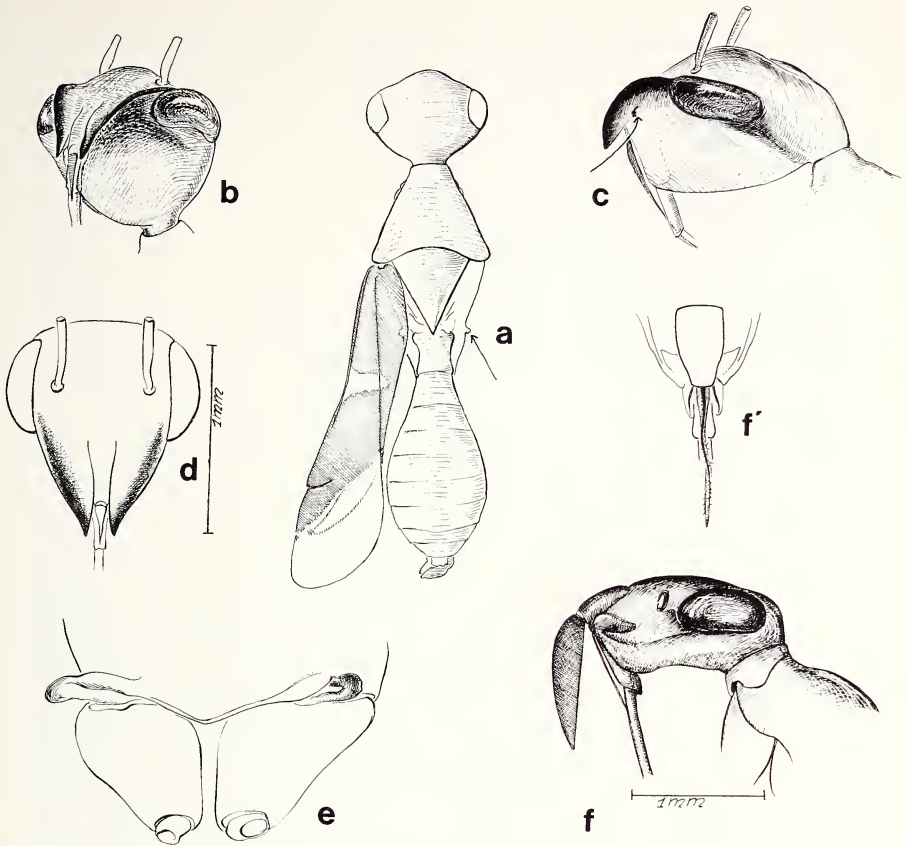


Fig. 2. a-e, *L. belua*, ♂; a, dorsal aspect; b-d, head viewed from different angles in order to show the mandibular-like projections of the genae; e, metathorax, ventral view, evaporatory area in front of metacoxa. f, lateral view of head and thorax of unidentified species (male) from Tanzania (Longido, Masai Distr., 1,500 m, 19.IV.1957, in Musée Royal de l'Afrique Centrale, Tervuren, Belgium); note the enlargement of the labrum, which is shown in dorsal view in f'.

## DISCUSSION

The biological significance of antlike habitus in many Miridae is a matter of speculation. In the absence of experimental evidence to confirm a selective advantage for the "ant mimics," the only valid neutral term for the phenomenon, as it manifests itself to us, would be myrmecomorphy and the respective bugs myrmecomorphic. The suggestion that the mistletoe mirid *Phoradendrepulus myrmecomorphus*, described recently by Polhemus and Polhemus (1985), in the subfamily Phylinae but not assigned tribe, is myrmecophilic because it is invariably taken in the company of *Crematogaster* sp., is premature.

It may be relevant to focus here on the lengthy discussion of this subject by Kullenberg (1946:10-16, 481-491) in his classic work on the biology of Northern

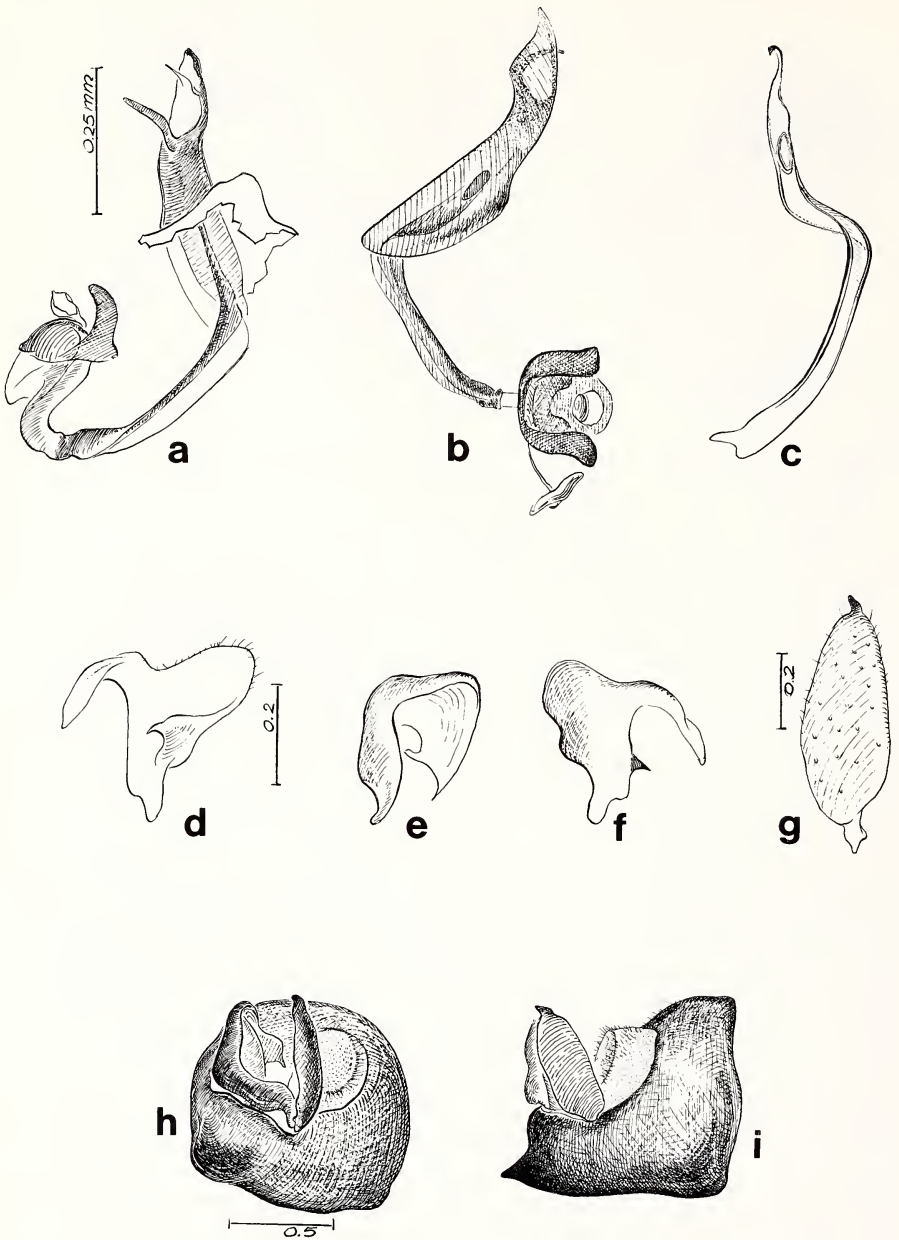


Fig. 3. Male genitalia of *L. belua*. a, b, phallus and phallosome; c, vesica; d-f, different views of left paramere; g, right paramere; h, i, genital capsule, phallus removed; h, oblique dorsal view; i, right lateral view.

European Miridae. The German language is possibly the reason that no reference is made to it in English literature dealing with the topic of ant mimicry. In Northern Europe, the ground-dwelling thermophilous *Myrmecoris gracilis* and *Systellonotus triguttatus* are the most striking myrmecomorphic species of the 90 species studied by Kullenberg. It cannot be denied that the uniformly brown micropterous specimens look superficially very antlike (Fig. 4a, b). *Myrmecoris gracilis* belongs in the Mirinae, Pithanini, and nearly all its attributes have been involved in changes of the basic body plan. Whereas "ant mimics" of other subfamilies show extreme modifications of the pronotum, sometimes much more excessively than appears from Figure 1, it is the mesothorax in *Myrmecoris* that produces the nearly hour-glass shape of the thorax (Fig. 4a, a'; note the displacement of the wing bases far back from the pronotum). I was further surprised to find that the labrum is enlarged in the vertical plane (Fig. 4a'), thus showing a tendency towards "false-mandible formation" ultimately realized in the African mirid illustrated in Figure 2f.

What kind of biological evidence do we have that might support our intuitive feeling of functional ant mimicry of these two European mirid bugs? I summarize here the observations and interpretations of Kullenberg (1946). Of all the species studied, *M. gracilis* and *S. triguttatus* have the strongest need for animal food<sup>2</sup>, which consists in the field predominantly of aphids; they certainly are not myrmecophagous as was suggested in older literature. The bugs show no special preference for aphid colonies that are visited by ants. If ants encounter the bugs in aphid colonies, the bugs will invariably be chased away; in insectaries they were always killed by the ants. The two color forms in *M. gracilis*, which are said to each mimic a different species of *Formica* (Reuter, 1879; Wagner and Weber, 1964:78), are considered by Kullenberg to be of no significance regarding protection against ants. The behavior of the bugs is very agile with rapid motions of the antennae, which are not bent in the ant-like fashion. Kullenberg preferred to restrict the term myrmecomorphy (his "Myrmecoidie") exclusively to shape and color and not to behavior, because there are nonmyrmecomorphic mirids that show ant-like behavior (he did not present examples). The protecting role of the antlike habitus against predators (birds, spiders, or insects) was greatly doubted by Kullenberg, but he did not provide evidence to the contrary. In the field he had not observed any predator acting on the myrmecomorphic bugs and he had not carried out experiments with potential predators. The fact that "normal" looking mirids became alert when an ant was approaching but behaved indifferently to antlike bugs led Kullenberg to suggest that something other than optical stimuli (e.g., substrate vibration, chemical stimuli) was more important to the insects ability to discriminate between ants and harmless antlike insects. On the other hand, the same author referred to experiments of Palmgren (1937) in which it was shown that five insect-eating birds avoided eating ants and also refused one antlike spider. One individual bird later learned to discriminate between ants and spiders and accepted the latter readily. The final conclusion of

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<sup>2</sup> It is generally assumed (e.g., Schuh, 1974) that most if not all clearly ant-looking mirids are mainly carnivorous. Interestingly, the second Pithanini in NW Europe, *Pithanus maerkeli* H.-S., which is much less antlike than *M. gracilis*, is 100 percent phytophagous.

Kullenberg (1946) was that there was no valid argument for the selective advantage of antlike form in the Miridae; he declared the biological meaning of myrmecomorphy as completely open for testing; one feels from his reasoning that he considered the antlike facies to have been evolved by process of chance.

Still, I think that any heteropterist who is impressed by the multitude of antlike forms paralleled in various families, implicitly feels that such bugs must have or have had great selective advantages because of their antlike appearance. We had to wait about 40 years after the comments of Kullenberg and other authors before more meaningful data with respect to the selective value of ant mimicry in bugs became available, albeit not yet in Miridae. The recent data are assembled from detailed observations on, and experiments with, two species of *Hyalymenus* in association with large complexes of ants in Brazil (Oliveira, 1985). The situation in these Alydidae is different from Miridae in two respects. Only the larvae are myrmecomorphic and diurnal; the adults are not antlike and they are mainly nocturnal. Both larvae and adults feed in aggregations on reproductive parts of plants. One of the alydid species studied lives on plants belonging to several families, including composites; the other species consumes sap only from solanaceous flowers and fruits. Many ant species forage on the same upper parts of these weeds, mostly feeding from honeydew-producing homopterans. The myrmecomorphy of the bugs is enhanced by antlike behavior, notably rapid zig-zag locomotion, constantly agitated antennae, and up and down movement of the abdomen. Oliveira is convinced that the larvae of the bugs under investigation act as mimics of certain ants and his data seem indicative of such relations. He suggests that the color and size changes through different larval instars "allow the immature bugs to mimic, during their development, different castes of a given ant model, as well as differently sized and coloured ant species." In one area a particular fourth instar color morph of one of the two bug species is considered as a species-specific mimic of one ant species. The last instars of the same alydid species are dimorphic, black or yellow. The proportions of these are different in two areas, matching the significant differences between color patterns of both ant faunas. The behavioral interactions between *Hyalymenus* larvae and the supposed ant models in the field, as described by Oliveira, are suggestive of a more or less tolerant attitude between both partners, whereas other ants evoked conspicuous avoidance reactions. Interesting as these results are, counts of the proportions of morphs between populations of the supposed mimics in relation to ant composition have to be extended over longer periods of time. The survey made to assess the stated correlation was apparently done only once, considering the rather low number of bug larvae counted. To test the hypothesis of Oliveira that larvae of *Hyalymenus* gain Batesian or Müllerian protection by resembling available ant models of different Müllerian complexes needs further extensive research. The only experiment with potential non-ant predators of the bugs was done with a praying mantid occurring in the same habitat. In captivity, the mantid attacked adult *Hyalymenus* but avoided encounters with the larvae, as well as with ants. These observations, however, are based on a few trials with only one mantid individual.

Returning to the myrmecomorphic mirids, one would be very lucky if some basic data as for alydids were available. That even weakly myrmecomorphic mirids have some profit from this resemblance may be assumed, but in order to prove it, the advantage must in some way be measurable. This would be very difficult or even

impossible if the original biotic circumstances changed in such a way that the model-mimic system no longer exists. One of the characters shared by many unrelated groups of often ground-dwelling mirids, whether they are weakly or strongly myrmecomorphic, is the wing pattern: brownish with a contrasting white hemelytral fascia. Since in other families this pattern often occurs with other myrmecomorphic traits (e.g., in Lygaeidae, Slater, 1982; in Saldidae, 3 times independently, Cobben, in press), it might be possible that the wing design, on its own or combined with behavior modification, grants some initial protection against certain predators. As is apparent from the observations of Kullenberg (1946), gaining insight into the selective value of a reasonably well-developed ant-mimicry system in the Miridae will be much more difficult than in the Alydidae. It would be more feasible to address the problem of mimicry in striking examples such as *Leaina belua* or other African hallo-dapines. If such species indeed appear entirely dependent on living aphids, they would be the direct competitors of aphid-milking ants<sup>3</sup>. It seems inconceivable that *L. belua* with its extraordinary cephalic adaptations and short rostrum (Fig. 1) could interfere with trophallaxis among ants, but then results of modern research on mimicry sometimes have exceeded our wildest expectations. Chemical interference with ants also is not *a priori* excluded. Typical ant-mimetic mirids have tuberculate outlets of the metathoracic glands (Figs. 2e, 4a, arrow), whereas a quick survey of my collection of Dutch mirids showed that the evaporative areas in nonmimics do not project from the thoracic sides<sup>4</sup>. Field observations and experiments on such aspects have to be done where such peculiar mirids live in Africa or other tropical regions. I hope that such studies can be undertaken before drastic environmental changes make them impossible.

There is another reason why heteropterists should study hallo-dapines. During a field study in Ethiopia in 1969, I collected *Haloldapus albofasciatus* (Motschulsky) everywhere in the environment of Jimma (Kaffa Prov.). This species (about 3 mm long) is ground living, preferring fallow land and has a very wide distribution in the Old World tropics (Schuh, 1974, 1984). Although a typical hallo-dapine with a transverse white fascia on castaneous-brown wings, it is not particularly antlike. About 80–90% of the females I collected were brachypterous, the hind wings reduced to stubs.

From a rough inspection of testis squash preparations made in Jimma, I concluded that this species revealed a karyotype of  $2n = 4$ . Last larval instars and adults were

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<sup>3</sup> In this connection it is relevant to quote an important comment of A. Akingbohunge (pers. comm.): "Rather amazingly, several isometopines of the tribe Myiommini from Asia and tropical America show varying degrees of modification of the facial plates, not too far removed from being a progression towards development of 'false mandibles.' For example, in *Totta* Ghauri from India, the tylus projects prominently forward over the base of the rostrum very much like lateral facial plates (i.e., genae, bucculae) that become modified and projected forwards (see Henry, 1980, Proc. Entomol. Soc. Wash. 82:178–194). As isometopines are now commonly associated with scales as predators, and scales are often tended by ants, your hypothesis on functional false mandibles may probably apply to them too!"

<sup>4</sup> However, A. Akingbohunge and R. T. Schuh inform me that protruding outgrowths of the scent glands do not occur in all ant-like mirids, whereas tuberculate outlets are also present in some non-myrmecomorphic taxa such as *Fingulus*, *Angerianus*, and *Stethoconus*.



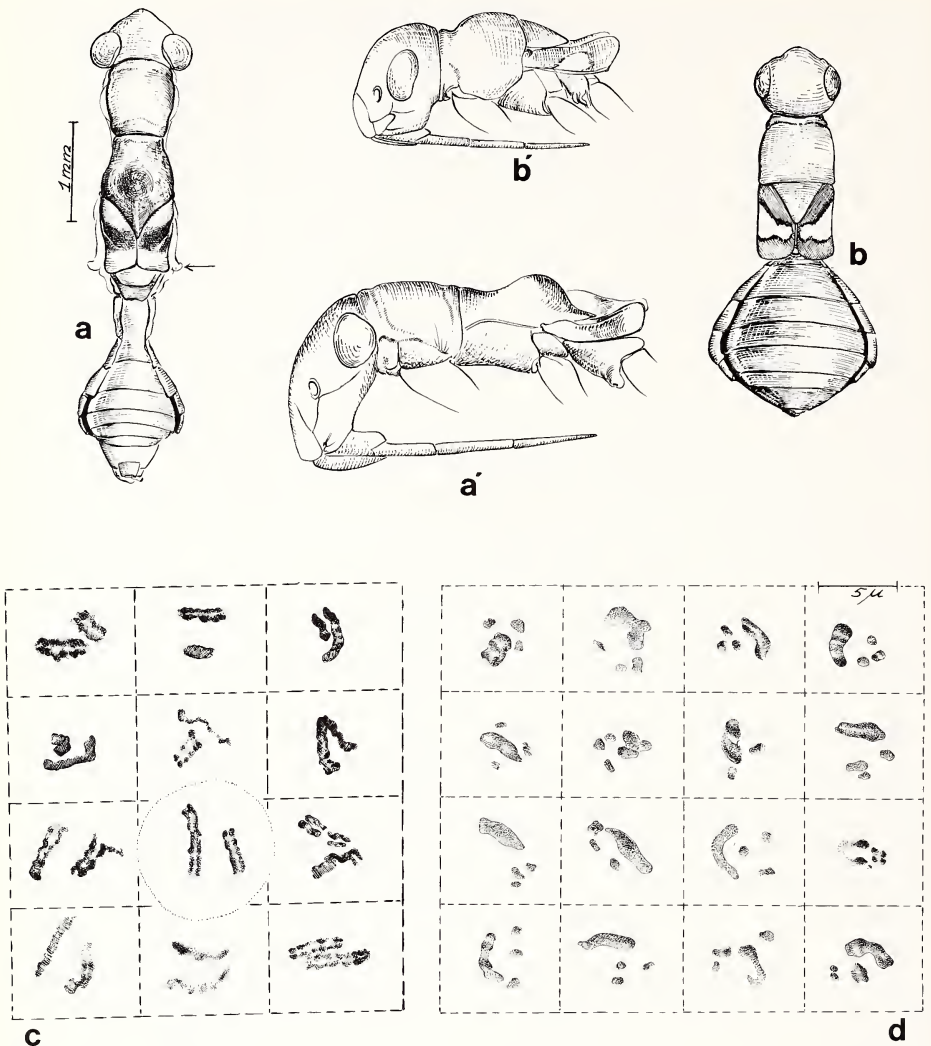


Fig. 4. a, a', *Myrmecoris gracilis*, dorsal and lateral views, respectively; b, b', *Systellonotus triguttatus*, idem. c, d, chromosome numbers in *Hallodapus albofasciatus* (c) and *Systellonotus alpinus* (d) testes, metaphase I.

transferred to Wageningen and kept alive for several weeks on a diet of wounded but still moving *Drosophila* flies. Again the chromosome number of several males was investigated, which consistently appeared to be two, very rarely three, haploid (Fig. 4c). This is the lowest number known in Heteroptera. Cytological data are now available for more than 900 species of Heteroptera in all families except a few (review in Ushima, 1979, and later references). There is only one other species known with  $2n = 4$ , viz., an unidentified *Lethocerus* sp. from Michigan. Since some other *Leth-*

*ocerus* spp. have numbers up to 30, it has been suggested (Chickering and Bacorn, 1933; Ueshima, 1979) that the x and y have both been translocated to one pair of autosomes and that fusion has occurred between pairs of autosomes. Although fusion of holocentric chromosomes is considered a rare phenomenon in comparison with fragmentation (Ueshima, 1979), the situation of  $2n = 4$  in *H. albofasciatus* cannot be explained other than by fusion. The known diploid range in Miridae (73 genera, 167 species studied) is 14 to 80; 80 is the highest number in the Heteroptera. Two species of Hallodapini, one from Japan and the other from USA investigated by other authors, have  $2n = 26$  and 34, respectively. The modal number of the subfamily, to which this tribe belongs, appears to be  $30 + xy$  (17 genera, 37 species; Ueshima 1979). Another myrmecomorphic hallodapine from Switzerland (*Systellonotus alpinus* Frey), which I have examined, also deviated from this general pattern because it possesses 8 chromosomes in the diploid state (Fig. 4d). If chromosome reduction would appear to be more widespread in the hallodapines, further extensive studies would be of great importance to cytologists interested in modes of chromosome change.

It is difficult to see any direct connection between the karyological phenomenon mentioned and myrmecomorphy. There might, however, be an indirect relation, as chromosome reduction would appear to be associated with the type of sexual dimorphism commonly found in myrmecomorphic Phylinae: males always macrop-terous, females usually brachypterous or micropterous. I am not aware of any such correlation in other insect orders. It is unfortunate that Microphysidae, which show a consistent striking sexual dimorphism in wing development, belong to one of the very few heteropterous families of which karyological data are entirely unknown.

#### ACKNOWLEDGMENTS

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